Proceedings of the American Academy of Arts and Sciences.

Vol. XLVIII. No. 20. — May, 1913.

CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE. — No. 236.

THE STRUCTURE OF THE GORGONIAN CORAL PSEUDOPLEXAURA CRASSA WRIGHT AND STUDER.

By Wayland M. Chester.

CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE. — No. 236.

THE STRUCTURE OF THE GORGONIAN CORAL PSEUDOPLEXAURA CRASSA WRIGHT AND STUDER.[1]

By Wayland M. Chester.

Presented by E. L. Mark, March 12, 1913. Received April 5, 1913.

CONTENTS.

Introduction	737	Dorsal mesenterial filaments	759
Methods	740	Growth	760
General structure	740	Muscles and nerves	760
Ectoderm	747	Skeleton and axis epithelium	762
Mesogloea	751	Summary	768
Endoderm	754	Bibliography	770
Structures concerned in nutrition	757	Explanation of plates	773

Introduction.

Pseudoplexaura crassa is found on the reefs of Florida, of the West Indies, and of the Bermuda Islands. It is very abundant in the shallow water of the inner reefs of Bermuda, and is there one of the two or three very common sea whips; but it is found in the deeper waters of the outer reefs as well. The range in depth, to include the greater number of colonies, is from a position near the surface at low water to seven or eight meters.

Ellis and Solander (**1786**) described this colony under the name of Gorgonia crassa. Kölliker (**1872**) placed under the name of Plexaura branched, sea-rod forms in which the polyps completely retract into a comparatively thick coenenchyma, in which club-shaped and spiny spindle-shaped spicules appear. The different species were divided into two groups: Plexaura durae and Plexaura molles. Hargitt and Rogers (:**01**, p. 285) follow Verrill ('**65**, p. 34) in describing this form as Plexaura crassa. Wright and Studer ('**89**, p. 141–143), from observations of Bermuda specimens, created for this species a new

[1] Contributions from the Bermuda Biological Station for Research. No. 27.

genus, Pseudoplexaura. The new genus is characterized by them as follows: "axis horny, with a central calcareous portion, the outer layer of coenenchyme is soft and when dry friable; the inner layer contains a number of light purple or violet coloured irregularly stellate spicules or spindles with few rays." It is to be distinguished from Plexaura, in addition, by the following features, among others: colony feebly branched, older portions of horny axis solid, younger portions with calcareous particles in the center; polyps placed close together in an irregular spiral, completely retractile tentacles without spicules or having a circlet of them at their base; spicules mostly spiny spindles, with numerous pink stellate forms and a few club-shaped with attenuated foliaceous expansions.

The important characters of the colony are: the relative smallness of the spicules; spicules in the outer cortex, and irregularly stellate forms in the inner cortex; the massing of the latter to such an extent as to make the inner cortex firmer when dried, while the outer is friable; the absence of spicules in the tentacles and polyps; the sluggish but complete retraction of the polyps within the cortex; and the smooth cortex surface without projecting calyces in the contracted or dried colony. The polyps are numerous. When they are completely expanded the tentacles of adjacent polyps overlap, and the coenenchyme is hidden. Each tentacle has ten to twelve pairs of pinnae.

Of the three groups of alcyonarian corals,— Alcyonacea, Pennatulacea and Gorgonacea,— only representatives of the first and second have had their minute structure studied recently; the Gorgonacea, to which Pseudoplexaura belongs, have received little attention except from von Koch ('87) in his very important but early comparative study. Studies on the Alcyonacea have been relatively numerous. Von Koch ('82[a]) described briefly the structure of Clavularia and other alcyonacean forms. Bourne ('95) described Heliopora coerulea and later made a very complete study of the origin and structure of its skeleton ('99). Ashworth ('99) studied the minute structure of Xenia Hicksonii Ash. and Heteroxenia elizabethae Köll. He found gland cells in the stomodaeum and correlated their presence there with the absence of the ventral and lateral mesenterial filaments. Hickson ('95) has given a detailed account of the cell structure of Alcyonium digitatum, and Pratt (:05) has described the digesting and mesogloea cells in several members of the Alcyonidae. She found a relatively large number of granular gland cells in the stomodaeum of feeding colonies and very few or none in starved ones. She

held the mesogloeal network of cells to be neuro-phagocytic in function. By feeding with colored material, she proved the ingestion and the carriage of such material by the amoeboid movements of the mesogloeal cells. Kassianow (:**08**) reviewed the literature for the muscle and nerve systems in Alcyonaria digitatum, studied these systems and described in detail the cells of the ectoderm, endoderm and mesogloea with reference to them. He denied a nervous function for the neuro-mesogloeal cells of Pratt.

Among the Pennatulacea, studies have been made by Korotneff ('**87**) and by Bujor (:**01**) on Veretillum. They described the cells of the ectoderm and endoderm carefully.

The only complete study of the cell structure of representatives of the group Gorgonacea is by von Koch ('**87**), who made a comparative study of the structure and minute anatomy of the forms found in the Bay of Naples, giving most attention to Unicella (Gorgonia) cavolinii.

Wilson ('**84**) studied the mesenterial filaments of a number of species representing the three groups. He described the difference in structure of the ventral and dorsal mesenterial filaments and the origin of each from different germ layers.

Bourne ('**99**), in a paper giving the result of his study of the origin of the skeleton in Anthozoa, describes the origin and minute structure of the alcyonarian spicule and the structure of the massive skeleton of the alcyonarian Heliopora. He further studied the structure and origin of "holdfasts," or desmocytes, in Heliopora, as well as in madreporarian forms.

Woodland (:**05**) reviewed the literature on the origin of the alcyonarian spicule and made a very complete study of it for Alcyonium. The names of von Koch ('**78**, '**82**[b]), Studer ('**87**, :**06**), and Alfred Schneider (:**05**) are important in the history of researches on the origin of the horny skeleton. Kinoshita (:**10**) has seen the origin of axis epithelium in young forms of Anthoplexaura and has confirmed von Koch's account of its ectodermal origin in the young form.

The study of this gorgonian coral (Pseudoplexaura crassa) was pursued during the summers of 1909 and 1910 at the Bermuda Biological Station for Research, and during the winter of 1909–1910 at the Zoölogical Laboratory of Harvard University. I wish to express my great indebtedness to Dr. E. L. Mark, the Director of these Laboratories for guidance and generous assistance.

Methods.

Small colonies were kept alive in large aquaria of running water for a short time. Small tips, 5 to 10 cm. long, were easily kept in smaller dishes of running water, if care was taken to keep them upright. Both Bouin's fluid and a five per cent formalin were successfully used as fixing agents. The fixing fluids were taken in some instances to the reefs and large tips or other pieces cut off from the colony and quickly transferred to the fluid; upon returning to the laboratory these were cut into small pieces. Both neutral formalin and Vom Rath's picric-osmic-acetic-platinic chloride fluid were used for nerve fixation. Corrosive sublimate and Wilson's fluid were both used, but did not give any better results than the formalin or Bouin's fluid. Decalcification was effected by 1 % acetic acid in absolute alcohol. Maceration by Hertwig's method gave good results. Delafield's haematoxylin and iron-alum haematoxylin could be used with decalcified material. Many sections of the soft tips were made without decalcification; but in these the haematoxylin overstained the spicules and the axial skeleton, obscuring the neighboring cells. By far the best general stain for these was Mallory's phospho-tungstic haematoxylin, which stained well after formalin and better after Bouin's fluid. This has the advantage that, while it does not obscure the spicules, it differentiates other structures.

General Structure.

A colony of Pseudoplexaura crassa presents a loosely divided group of long branches on a short stem; or the short stem may have short branches which divide and divide again, terminating in long whips. A drawing of a very young colony (Fig. A) illustrates the character of the branching. The short basal shaft spreads out on the coral rock or on old coral masses, secreting a skeleton that becomes very firmly attached to its substratum. The whips, which rise in many planes, are cylindrical, long and flexible, and taper somewhat gradually to the tips, which, however, end bluntly, or even with a slight enlargement. The brownish polyps stand at right angles to the branches (Plate **1**, Fig. 1), closely crowded against one another, except at the tips of the branches, where the coenenchyma can often be seen even when all the polyps are expanded. Because the polyps when

expanded stand at right angles to the branches, and are crowded, the colony in this condition looks like a miniature leafless shrub with unusually thick branches; because the tip is often bare of polyps or these are there contracted, the colony when seen at a distance below the surface may resemble very superficially a huge compound

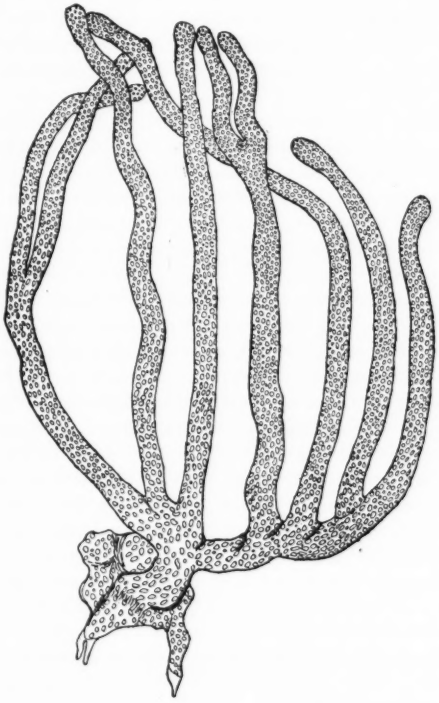


Fig. *A*. Young colony of Pseudoplexaura crassa, showing method of branching and the calycle openings in the coenenchyma.

tube sponge. But Figure *A*, although it shows the character of the branching, does not show the great number of branches, or whips, that occur in larger forms. As found on the Bermuda reefs, the species varies greatly in size. A small colony stood 90 cm. high, its terminal 60 branches spreading over a circle 60 cm. in diameter. Another

colony was 110 cm. high with 250 terminal branches. A third measured 200 cm. in height and had 300 terminal branches. These three, taken from one place, are representative of the forms inside the outer reefs. On the outer reefs, forms 225 cm. high have been found. In the first colony (90 cm. high) the diameters of the stems were measured. Half way between the ground and the tips, with the polyps fully expanded, the branches were 4 cm. in diameter; at the base, 5 cm., and near the tip, a little more than 3 cm. After the polyps were fully contracted, the measurements were 1.5 cm. for the base, and .5 cm. for the tip.

A transverse section of a branch, or whip (Plate **1**, Fig. 1), shows the structure. In common with that of the branches of Gorgonacea generally, there are recognizable three zones: a central axis of skeletal material (*ax.*), a fleshy enveloping layer,— the coenenchyma,— and a zone of polyps. The polyps can completely retract into spaces in the coenenchyma, whereupon two zones only are evident. The horny axis is very hard at the base but quite soft at the tip of the branches and, except at the basal end, is very flexible. To the naked eye, it is composed of two parts, a central, soft marrow, light in color (white in the figure), and an outer, harder, brown or black tubular shaft or cortex. The marrow has nearly the same thickness in all parts of the colony.[2] While its diameter is sometimes slightly smaller at the tip, it is not always so. Its variations are not wholly dependent on age, for it is slightly larger or smaller in parts of the stem and these parts occur irregularly. It is composed of a number of chambers filled with loosely branching threads (compare Plate **4**, Fig. 58), and having walls of horny material, the chambers being generally arranged one above the other (Plate **4**, Fig. 57, *med. ax.*). The loosely branching threads in the chambers are not shown in this figure, but are seen in the small chamber of the axis-cortex shown in Figure 58. The walls of the medullary chambers are very thin. Those of the axis-cortex chambers are very thin at the tip of a branch, while at the base they are very thick and hard. This is due to the fact that while the marrow chambers are laid down axially (i. e., at the end of the axis) in the branch, the cortex grows radially. The latter is composed of smaller chambers, which in longitudinal sections appear crescent shaped (Fig. 57, *ctx. ax.*). Not only is the cavity smaller, but the walls are thicker than those of the marrow. The first crescents laid down are adjacent to the marrow and very short, but as the axis-cortex increases in

2 This cortex of the axis will be called axis-cortex to distinguish it from the more superficial coenenchymal cortex.

thickness, the outer ones are very long and have much thicker walls and thinner cavities. To the naked eye this gives the appearance of a solid cortex.

Where a branch is formed there is a break between the marrow of the branch and that of the stem (Plate **4**, Fig. 61), and the axis-cortex forms a thick knee-like union at the stem for strength. At the base of the colony the axis-cortex is spread upon the substratum and the marrow is lacking. Many of the Bermuda colonies that were located on the shallow reefs, where the tips were exposed at the lowest tides, had lost the fleshy envelope of the tips of the branches for the distance of a few centimeters, the horny axis being here covered by diatoms. The fleshy coenenchyma was growing loosely around the old axis and taking the shape of the original branch. In such regenerated tips no new marrow was formed. In a few instances the old axis had been completely covered, but the coenosarc had not grown enough beyond the axis to give evidence of the presence or absence of a marrow distal to the old dead axis.

The coenenchyma is composed of two regions, an inner, exhibiting longitudinal canals, and an outer, containing the calycles or polyp-chambers. The longitudinal-canal region is characterized by a number of large canals running parallel to the axis (Plate **1**, Fig. 1, *can. lg.*), and by the presence of purple, irregularly stellate spicules (Fig. *B*, 5–7) loosely massed in groups (*spc.'*). The spicules are represented diagrammatically in the left half of Figure 1, to show their positions. The longitudinal canals are less numerous at the tips of the branches — where there may be eight to ten — than they are at the bases, where twenty or more may be found. The diminution in number from the base to the tips is due to the running together of two adjacent canals or to the abrupt ending of one or more. Some of them run continuously from the basal half of the stem into the lower (abaxial) face of a branch. On the axial face of the branch they may be continuous with those of the stem, or the canal may begin abruptly in the branch without such connection. At the tips and on the branches the longitudinal canals connect with one another and with the polyp cavities by smaller canals (*can.*). At the base of the colony they run out radially and end blindly, or are connected with one another or with polyps by the smaller canals. At the tips the purple spicules are loosely arranged in two concentric cylinders separated from each other by the zone of canals. Where the branches are older, however, the inner cylinder breaks up into small groups, which lie between the axis and two adjacent canals (Fig. 1, *spc.'*); here the spicules interlock

in a close mass. The diagrammatic nature of Figure 1 does not permit one to show the closeness of the interlocking of these spicules.

The outer region of the coenenchyma is a thick zone with polyp chambers (*cam. pyp.*), into which the polyps can completely retract. These chambers communicate with each other by a greatly branched system of small canals (*can.*). These canals are represented in only one half of Figure 1 (Plate **1**). The actual canals are much more numerous and are more complexly branched than the diagram shows. Between the chambers white spindle-shaped and spiny spicules (Fig. *B*, 1–4), longer than the purple ones of the inner region, are found (*spc.*). Some of the deeper of these may be purple. Indeed there is considerable variation in both color and form of the spicules of different colonies and even of the same colony. These spicules have been described and figured by Wright and Studer ('**89**), by Hargitt and Rogers (:**01**) and by Verrill (:**07**). Figure *B* gives the relative proportions in size, as well as the differences in shape for the spicules of both the inner and outer regions of the coenenchyma. Figure *B*, 5–7, presents spicules of different shapes found near the long canals, where they are often locked together. In Figure *B*, 1, 2, are seen long white forms from the outer part, and in Figure *B*, 3, 4, spicules from the deeper part of that region.

The polyp-zone consists of the exposed part of the polyps or anthocodia (Fig. 1, α–γ). These when expanded are cylindrical. The mouth is oval and the eight tentacles of the crown stand at right angles to the column. The tentacles are conical, relatively long when fully expanded, and carry ten to twelve pairs of conical pinnae, arranged in two longitudinal lines, one on either side. No spicules are found in the polyps.

The anthocodia are brown and, when expanded, give the colony its prevailing color, which is caused by the presence of the Zooxanthellae (Plate **2**, Figs. 20, 21, *zox.*) that crowd the endoderm cells and give a lighter or darker brown color in accordance with the degree of the animal's contraction. A little magnification shows that each disk is white and also that along the eight longitudinal lines corresponding to the union of the mesenteries with the body wall the color is white. The white appearance in both cases is due to the absence of these algae. The color of the coenenchyma between the anthocodia is distinctly white because of the absence of Zooxanthellae near the surface and the presence of white spicules.

The wall of the column of the anthocodium (Plate **1**, Fig. 1, β) merges into that of the somewhat larger chamber in the coenenchyma

and its endodermal epithelium is continuous with that of the chamber. The stomodaeum (Fig. 1, η, *stmd.*) is long, reaching when the polyp is expanded, nearly if not quite to the level of the surface of the coenenchyma; it is broadest in the dorso-ventral plane and has at its ventral angle a prominent siphonoglyph (Fig. 2, *sipy.*), which is not

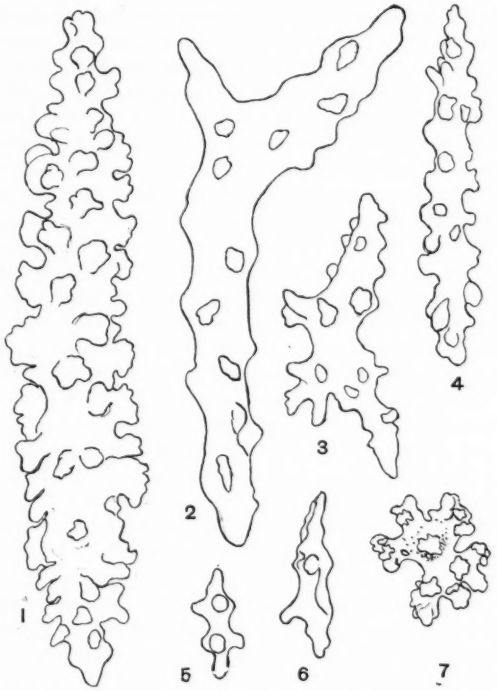


Fig. *B*. Calcareous spicules: × 90. 1–4, white spicules of outer cortex region; 5–7, purple spicules from the region of the longitudinal canals.

visible on the disk, but reaches nearly to the deep end of the stomodaeum. The structure is that usually found in the siphonoglyph of Alcyonaria. A transverse section through the stomodaeum is shown in Figure 2. The siphonoglyph is always ventral, and the longitudinal muscles of the eight mesenteries, as is usual in Alcyonaria, are located on the ventral sides of the mesenteries. Figure 3 shows a

section made below the level of the first cut and near the level of the lower end of the stomodaeum — but still through the anthocodium — very close to the coenenchyma. The mesenterial filaments are cut in this section. The filaments belonging to the six ventral and lateral mesenteries are very short (never more than two millimeters long, and usually less than one), and appear as very slight thickenings of the edge of each mesentery. The filaments of the two dorsal mesenteries are seen to be deeply grooved; they are very long and pass with the mesentery from the stomodaeum to the very base of the chamber, being much convoluted at their lower ends. The section shown in Figure 4 is cut through the lowest part of the polyp cavity. The ventral and lateral mesenteries here have no filaments, but the dorsal filaments, cut across several times, show their grooved condition. In the lower region of the polyp chamber are also many ova, or else (the colonies being dioecious) masses of sperm mother cells covered by the endoderm. The ova are attached singly to the sides of the six ventral and lateral mesenteries. The eggs in July were large, but there was no evidence of fertilized eggs or of matured sperm.

Phases in the retraction of the polyp have been described by Wright and Studer ('89) and appear to be similar to those of Alcyonium (Hickson, '95). When the colonies were transferred from the conditions of the sea to those of the laboratory, it was seldom that they remained as fully expanded as at first. The polyps were appreciably shorter, but they had the shape and character described (Plate 1, Fig. 1, α). Sometimes the mouth was open and observation showed a slight current of water passing into the stomodaeum; at other times, or in other parts of the colony, the mouth was tightly closed. Sometimes the tentacles and pinnae were contracted to form eight short cones at the top of a column comparatively well expanded, the mouth being either open or closed. A circular constriction of a narrow region then appeared just below the disk, while the remaining part of the body bulged like a flask (Fig. 1, γ). A slow withdrawal of the polyp then occurred, evidently by means of the longitudinal muscles of the mesenteries, together with a slow inturning of the tentacles, until the disk and tentacles were at the level of the calycle. These now drew within and the oval or ovate calycle opening became visible (Fig. 1, δ). Sometimes in this method of contraction, the tentacles were first rolled toward the mouth, giving the disk and tentacles the appearance of a circle with eight indented radii (Fig. 1, β). The column was then contracted into the polyp cavity of the coenenchyma, as already outlined. But this method of contraction is not the invariable rule.

Sometimes, although the tentacles are contracted, the mouth remains open and the column is brought down nearly to the level of the coenenchyma, where it remains for a long time, the current of water to and from the stomodaeum evidently not being checked (Fig. 1, ϵ). Probably the coenenchyma is also capable of slight contraction and expansion, due principally to the action of the muscles of the mesenteries. When the tip of a branch is cut off, the coenosarc, with the polyps near the line of the cut, becomes appreciably of smaller diameter, thus partially covering the cut surface; and the same result is seen in the regenerating branches on the reefs, where the polyps have been turned from their radial position and are held in such a way as to lessen the area of the cut surface.

Ectoderm.

The ectoderm of the polyp wall in the expanded condition is more than one cell thick, showing an epithelial and a subepithelial part (Plate **2**, Figs. 8, 18). In the epithelial part, the cover cells (*cl. teg.*) are conical, with a round or polygonal external surface as a base and with the opposite end, as apex, extending into the mesogloea as a process. In the expanded state of the polyp many of the cells are peltate or mushroom shaped, since they have the appearance of an external plate supported by a rapidly narrowing stem. This stem soon takes a thread-like character and may be branched (Figs. 9, 11). The outer surface is often convex, like a mushroom, but it may be indented, so that the section of it is cusp like (Fig. 18, *cl. teg.*). In the expanded condition of the polyp, the plate-like surface covers a relatively large area and the process becomes shorter; in the contracted condition, the cells approach a columnar shape, though the process is still thread-like at the mesogloeal end (Fig. 20, *cl. teg.*). The protoplasm is finely granular and sometimes large granules also occur (Figs. 10, 11). Although sometimes without vacuoles, these cells usually contain many small ones. The nuclei are large and granular and are situated in the outer half of the cells or near the point of the cusp. Among the covers cells are found nettle-cells or thread-cells with their nematocysts (Fig. 18, *nm'cys.*) and sense cells (*cl. sns.*).

The nematocysts are of two kinds. The larger and more numerous ones (Plate **2**, Fig. 18 and Plate **4**, Figs. 43–46) occur in batteries of six to ten, but they may be found in much larger numbers. The cyst is sharply outlined and is an elongated oval with a length three times

its greatest width. Its length varies from 10 to 14 micra when unexploded. Around the cyst is a thin layer of granular protoplasm containing the flattened nucleus of the cell at the region of the greatest width of the cyst. The nucleus stains deeply with basic stains, the chromatin being abundant and granular. There is no trace of a cnidocil or of a cytoplasmic process projecting from the free surface of the cell. After staining in Mallory's phospho-tungstic acid haematoxylin or methylen blue a thick thread may be distinguished within the cyst, though not easily. It passes in a zigzag line from its attachment for a third of the length of the cyst and fills the remaining two thirds of the cyst in a tight coil (Fig. 44). When exploded the thread is quite thick and short and without barbs. Nematocysts of the second type (Fig. 47) are not found so abundantly. They are ovate and much smaller than those of the first type. The length is 5 to 8 micra. The nucleus is at the broad end of the enclosing cell. The thread with four or five spirals is sharply outlined even without stains. Exploded, it is long and slender, without barbs.

Sense cells (Plate **2**, Figs. 8, 13, *cl. sns.*) occur among the cover cells, but are readily found only in the nematocyst batteries, where their bristle tips can be seen in favorable sections and where their nuclei reveal them by the size, which is smaller than that of the cover-cell nucleus. The sense cell is narrow and spindle-shaped with a long process extending into the mesogloea. Its protoplasm is slightly more evenly granular than that of the cover cells, though not greatly different from it; but its nucleus is small and round and can be readily distinguished from the larger nucleus of the cover cells. The bristle point is exposed between the cover cells, or between these and the nematocyst cells.

The subepithelial part of the ectoderm is made up of interstitial cells, globular cells with granules, nematocyst cells, and ganglion cells. It is not a sharply defined layer, since the cover cells and the sense-cell processes pass through it. The interstitial cells (Plate **2**, Figs. 18, 20, *cl. in.*) are globular or have a central body with branching processes. In fact, the cells, or some of them, may change their shape in an amoeboid manner. The cytoplasm is similar to that of the cover cells; the nucleus may be smaller, though it varies greatly in size. The granular cells are filled with comparatively large granules and stain sharply with eosin. They have the appearance of the granular cells found in the mesogloea of the coenenchyma. Besides cells containing fully formed nematocysts, there are some which show stages in the formation of the nematocysts (Fig. 18, *cl. nm'cys.*).

Other cells, lying close to the mesogloea with processes parallel to it, are interpreted as ganglion cells (Fig. 20, *cl. gn.*). The difficulty with this interpretation is due to the presence in the adjoining mesogloea of the mesogloeal cells, which sometimes resemble the supposed ganglion cells in shape. In preserved material, the fibers of these ganglion cells sometimes possess many minute varicosities. The cytoplasm is more evenly and closely granular than in surrounding cells.

The ectoderm of the tentacles (Plate **2**, Fig. 5) and pinnules (Fig. 6) is relatively thicker than that of the polyp wall, but shows the same superficial and deep layers. It also differs from that of the body wall in the smaller number of the large kind of nematocysts and in the presence of muscle cells in the ectoderm of the oral face of tentacle and pinnule. The deep end of the muscle cell (Figs. 16, 17) is elongated into a process which is perpendicular to the axis of the body of the cell, and runs lengthwise of the tentacle or pinnule. Each process contains in its axis a single highly refractive contractile fiber, or myoneme. The nucleus is small and finely granular. Usually the cell body is flattened in the plane of the muscle fiber; but the flattening may be at right angles to that plane. It is only occasionally that these muscle cells reach to the surface of the ectoderm and thus present the typical condition of an epithelio-muscle cell. Since all the muscle fibers run lengthwise of the tentacle, a transverse section of the tentacle (Fig. 7) shows, adjacent to the mesogloea of the oral surface and the sides, a very definite row of dots — the cut ends of muscle fibers. In sections dyed in Mallory's stain these fibers, being deeply colored, appear as dark dots, or, if cut somewhat obliquely, as short lines. In the partially contracted condition of the tentacle the dots no longer occupy a plane surface, for the originally plane surface is so folded that the line of dots is very sinuous, and even forms in some regions a series of pinnate figures.

The ectoderm of the polyp wall passes gradually into that of the coenenchyma, where, between the polyps, the cover cells (Plate **3**, Figs. 23, 24) are very long and conical, but never show the indented peltate shape seen in the ectoderm of the polyps. The ectoderm of the coenenchyma shows a thicker subepithelial region, which gradually merges with the mesogloea. As a rule, the interstitial cells are so numerous in the thick mesogloea and the mesogloeal elements are so near the long cover cells that it is hard to find a boundary between the two layers. The nematocysts of the larger kind are arranged in very large and numerous batteries; those of the smaller kind occur individually and are very few. Both kinds of nematocysts have the

same structure as those of the polyp wall. Sense cells, like those in the body wall and tentacles, are found in the batteries and increase in number with the increase in the number of cysts in the batteries.

Some of the ectoderm cells of the coenosarc between the polyps contain a prominent, highly refractive, homogenous fiber (Plate **3**, Figs. 24, 26, *fbr. sst.*), beginning near the nucleus and extending to the base of the cell, which is implanted in the mesogloea. The nature of these fibers is not perfectly certain, but it is probable that they are the same as the "Stützfasern" described by K. C. Schneider (**02**, p. 622) for Anemonia; however, I have never seen evidence of their fibrilation, such as Schneider has shown to exist in the case of typical "Stützzellen." Figure 26 shows the distribution of these Stützfasern in the coenenchyma and their relation to the grooves which occur in these regions.

The ectoderm of the disk is, in its content and cell structure, like that of the oral face of the tentacle. When the disk is fully expanded, the stomodaeal epithelium reaches over on to the disk. The siphonoglyph and the dorso-lateral regions of the stomodaeum are both characterized by extremely long columnar ciliated cells. The siphonoglyph (Plate **3**, Fig. 32) has neither gland cells nor nematocysts, both of which are abundant in the other regions of the stomodaeum (Figs. 30, 31). The columnar cells of the siphonoglyph are long and of small caliber; each has a single strong cilium, or flagellum, which is longer than the cell. The cytoplasm is finely and rather densely granular, and each oval or elongated nucleus has one or two prominent nucleoli and a small number of chromatin granules. The nuclei occupy different levels in adjacent cells and are so situated that collectively they form a definite layer. Four layers, then, are recognizable in the ectoderm of the siphonoglyph (Fig. 32): (1) subnuclear, composed of the bases of the columnar cells, between which may be found occasional nutrition cells (*cl. nut.*) and ganglion cells, (2) the nuclear layer, (3) the layer between the nuclei and the basal granules of the cilia, (4) the cilia layer, a wide border characterized by the long and prominent basal granules. No ectodermal muscle cells are found in this region.

In the dorso-lateral portion of the stomodaeum (Plate **3**, Figs. 30, 31) four types of cells occur abundantly, supporting cells (*cl. sst.*), mucus cells (*cl. muc.*), granular gland cells (*cl. grn.*), and the small nematocyst cells (*cl. nm'cys.'*). The same four layers as in the siphonoglyph are found, but the nuclear zone is much wider, and the cell bases do not always terminate so sharply against the mesogloea. The cilia are short. The supporting cells (*cl. sst.* and Fig. 39, Plate **4**)

are columnar, finely granular, with very small vacuoles, and with a short cilium that has a prominent, inverted cone shaped basal granule. The nuclei vary from oval to globular, but are more often oval, stain lightly, and have one or two prominent nucleoli. The mucus cells (Figs. 30, 37, *cl. muc.*) are columnar or flask like, not always reaching the full depth of the layer, sometimes staining evenly with eosin, at other times showing a loose network of protoplasm. This network stains deeply with muci-carmine. The nucleus is in the basal end, is globular or nearly so, and stains deeply. The granular digesting cells (*cl. grn.*) are very numerous in some colonies, few in others, and particularly few in starved colonies. They also are columnar or flask shaped with a small round nucleus, that stains lightly, near the middle of the cell. Large granules, staining deeply with haematoxylin, sometimes partly, sometimes completely fill the cytoplasm. Nematocyst cells of the smaller type (Fig. 31, *cl. nm'cys.'*) are abundant between the columnar cells in the cilia layer, but the cysts are smaller than those at the surface of the body. They are here nearly globular with a deeply staining nucleus at the lower end. The border, or cilia, region of the supporting cells (Fig. 39) sometimes shows the presence of variously shaped, but very small, digestive or nutritive granules. Below the nuclear layer and between the supporting cells are found many globular cells (Fig. 30, *cl. gl.'*), containing large granules that do not stain with haematoxylin. In a few cases these cells have shown karyokinetic figures. I interpret them to be young stages of gland cells and think they are the same as those described by Kassianow (:08). Ganglion cells are found not far from the mesogloea, but they are very few.

The dorsal filaments and the axis epithelium are described later in this paper.

Mesogloea.

The mesogloea is very thin in the body wall of the polyp and in the tentacles, as well as in the stomodaeum and mesenteries. The boundary between it and the ectoderm or endoderm is sharply marked wherever muscle fibers are found; where there are no muscle fibers the division is not clear. In the pinnules (Plate **2**, Fig. 6) evidence of mesogloea is seldom found, and even in the tentacle (Fig. 5) cells are not often seen imbedded in it. In the stomodaeum the layer is made out with difficulty, but it is thicker than in the tentacles. In the mesenteries (Plate **3**, Fig. 33) it is very evident, though thin,

being sharply outlined in regions where there are muscles; but only occasionally, and then in the thicker parts of the layer, are there any included cells. A thin layer of it is also found between the endoderm of the mesenteries and the egg or the sphere of sperm mother cells. In the body wall, particularly at the base of the polyp (Fig. 19), it is thicker and here a few included cells appear. These cells (*cl. ms'gl.*) are smaller than the ectodermal cells and have a correspondingly small nucleus; they have several elongated, more or less branched processes. Cells in the coenosarc (Fig. 28, *cl. ms'gl.*) which I interpret to be the same as these are very numerous and show plate-like expansions of the terminal branches, which have been described by Kassianow (:**08**, p. 525) for Alcyonium. The mesogloea layer in the coenosarc is very thick (Fig. 22); here the newer mesogloea, that which is near the ectoderm, is less dense than the portion which occupies the deeper layers. Sections stained in either eosin or Mallory's phospho-tungstic haematoxylin show well the differences between these regions. The ectoderm cells of the coenosarc are very long and the interstitial cells at their bases very numerous. The latter have the appearance of being pushed away from the ectoderm as growth proceeds, and they arrange themselves, or are arranged, in masses or cords (Figs. 22, 28, *cl.cd.*), in which the individual cells are often only loosely associated. The interstitial cells (Fig. 24, *cl. in.*) which are still near the ectoderm, are globular or irregularly branched, but otherwise they are not different in appearance from the ectoderm cells of the coenosarc or of the polyp wall and tentacle; but they, together with the deeper and more specialized cells constituting the cords (Fig. 22), reach down even to the axis epithelium. A transverse section of such a cord is given in Figure 29; other sections are shown in Figures 27 and 28. In these cords some of the cells (*cl. in.*) are like the interstitial cells near the ectoderm. Others (*cl. grn.'*) contain few or many granules, which vary in size and staining capacity, but always stain, either slightly or heavily, in haematoxylin or in eosin. The granules vary in size in different cells. In other respects these cells resemble interstitial cells. Some of the cells at the edges of the cord are partially surrounded by the jelly of the coenosarc, and these are appreciably smaller and more elongated than the others. The loosely arranged cells of the cord show no extra-cellular matter except at the edges of the cord. Where such matter is evident, the characteristic finely granular mesogloea cells (*cl. ms'gl.*) are to be found with their greatly elongated processes and terminal branchings.

I believe the cells enumerated below constitute a genetic series:

(1) the interstitial cells (*cl. in.*), or some of them; (2) the loosely arranged cells (*cl. grn'.*) with few granules, and those with larger granules; (3) the cells on the outside of the cords, which are either partially or wholly surrounded by secreted matter; and (4) the smaller mesogloea cells (*cl. ms'gl.*); because the interstitial cells and the series of loosely arranged cord cells are continuous with each other. The cells of each series may change their shape by amoeboid movements, as sectioned living material has shown me. Any of the cells, except the mesogloeal cells, may have granules. The cytoplasm and the nuclei of all these cells are alike, except in regard to the size and shape of the cell and nucleus and the presence of granules. But it would not be correct to argue from this series of cells found in the coenosarc that the mesogloea is of exclusively ectodermal origin. The bases of the ectoderm cells seem active in the formation of mesogloea in all parts of the colony and there is evidence of the secretion of the same substance by cells associated with the axis epithelium in the axis region. The evidence drawn from Pseudoplexaura does not exclude the probability that the endoderm is also active in the formation of mesogloea in the tentacle, polyp wall, and particularly in the mesenteries. The small cells at the end of my series of four given above occur in most abundance where the jelly layer of the coenenchyma is most dense; they simply represent, it seems to me, the ultimate condition of cells whose usefulness may not be limited to the formation of mesogloea, but which in all of the earlier stages have been more or less active in the formation of such substance.

But not all of the mesogloeal cells belong in this series, nor are all those in the cords secreting cells. Some of the interstitial cells develop nematocysts and some are spicule-forming cells. Those forming nematocysts are very abundant in the coenosarc, and not only are stages in the development of the cyst found, but cysts (*nm'cys.*) as large and as fully formed as any near the surface are very abundant, not only among the interstitial cells near the ectoderm, but also in the cell cords and in the deep parts of the coenenchyma. These, I believe, have been carried in from the ectoderm by the rapid growth of the outer layer and by the amoeboid action of the cells around them.

In growing regions at the tip of the branches some of the interstitial cells, pushed deeper by growth, secrete the spicules, probably during special periods. The formation of the spicules is not different from that described by von Koch (**'87**), Bourne (**'99**), or Woodland (**:05**). The more or less rounded spicule-cell first shows a small calcareous mass (Plate **3**, Fig. 23, *spc.*), which increases in size with the division

of the cell and takes on a characteristic shape (Figs. 25, 28). Several nuclei are to be found in the cytoplasm enveloping most of the spicules, thus showing that the spicule-cell usually divides more than once. Figure 25 shows the arrangement of the organic matter of the spicule after decalcification; this is similar to the condition described by Bourne.

Certain of the cells in the mesogloea (Plate **4**, Figs. 48–51) show ovoid or globular bodies similar to those described by Bourne ('**99**) and Woodland (:**05**) as possibly stages in nematocyst formation. Rounded nutritive cells also occur, sometimes few, but in the coenosarc of some colonies very abundantly. They are also found occasionally scattered among the ectoderm cells of the outer edge and also among endoderm cells, where they probably originate. They stain more deeply with eosin than the surrounding cells.

Endoderm.

The endoderm lines the coelenteric side of the stomodaeum, the disk, the polyp wall, the mesenteries and all the canals. It is composed of three types of cells; supporting, mucus, and granular gland cells. Muscle cells are found in some parts. The cell characters are similar in the endodermal lining of the anthocodia (Plate **2**, Fig. 20), the polyp chamber (Plate **4**, Fig. 56) and the connecting canals (not including the long nutritive canals). The supporting cells are narrow and columnar, in contact with each other proximally and distally. In partially contracted individuals (Fig. 20) the supporting cells and the less numerous gland and mucus cells appear crowded into close contact; but in slightly expanded individuals (Figs. 55, 56) after fixation frequent spaces occur separating individual cells except at their two ends. The cytoplasm is coarsely vacuolated. A large nucleus is found somewhere in the basal two thirds of the cell. The cells are sometimes crowded with Zooxanthellae (*zox*), which are usually very numerous in and near the polyps, but are not so abundant in the deeper canals. Three, four, or more of these algae are common in the sections of each cell in the tentacles, polyp wall or outer coenosarc. Each endoderm cell has a single weak cilium inplanted in its free end, and at its attached end a myoneme, which runs circularly in the wall of the anthocodia and polyp chamber, and generally so in the canals. Mucus glands are abundant (*cl. muc.*); they appear as columnar cells with the cytoplasm in the form of a

large-meshed reticulum that stains deeply with muci-carmine, and each has a darkly staining nucleus. There are occasionally found also gland cells (Fig. 55, *cl. grn.*) similar in character to the granular gland cells of the stomodaeum. The feeble staining of the nucleus and the presence of large granules in the cytoplasm show the likeness. The cells may be shorter or even spherical They are not limited to particular regions, but are scattered throughout the endoderm of the polyp wall, the canals and the mesenteries.

The endoderm of the polyp wall (Figs. 20, 55) has longer cells and stronger myonemes than that of the polyp chamber or canals. However, in the pinnules and in the tentacles, except at their very bases, the myonemes and the granular gland cells are lacking (Figs. 5, 6); otherwise the layer is here like that of the body wall.

The epithelial cells and the muscle elements of the endoderm of the mesenteries (Plate **3**, Fig. 33) are specialized, at least in certain regions. On the so-called ventral surface of the mesentery the longitudinal myonemes belong to cells that are entirely below the free surface of the epithelium. These muscle cells are long and spindle-shaped (Plate **4**, Fig. 38), with a small amount of cytoplasm enveloping the fiber (myoneme) and most abundant around the elongated nucleus. The cells are very numerous and the fibers are so arranged that in the cross section of the mesentery they form wavy rows of black dots adjacent to the ventral side of the mesogloea (Fig. 33, *my'nm.*). Other muscle fibers, that run radially on the mesentery, are found in both layers of the endoderm and their cells are epithelio-muscular, though in some cases the cell body may be slightly sunk below the surface. Where the endodermal epithelium covers the genital cells, the epithelial cells are shorter and bear no muscle fibers.

The endoderm of the longitudinal canals (Plate **4**, Fig. 59) has very long cells as compared with that of the other canals; they are, however, of the same type, viz. supporting cells; they are slender, columnar, vacuolated, and slightly separated from one another except at their proximal and distal ends. No muscle cells, or myonemes, are found in this endoderm.

As compared with corresponding structures in other alcyonarians, it may be said, in brief, that the ectoderm of Pseudoplexaura is like that of the other members of this group described by previous authors, in having an epithelial and a subepithelial layer; in the shape and character of its cover cells it is like Alcyonium (Hickson, '**95**, Kassianow,

:08), and is not greatly different in its cell characters from Xenia (Ashworth, '99) or Veretillum (Buvor, :01). The nematocysts of the larger kind are about the size of those of Clavularia (von Koch, '82[a]), and are generally slightly larger than those of Xenia or Alcyonium. Those of the smaller kind seem significantly numerous in the stomodaeum. Sense cells like those of Alcyonium (Kassianow, :08) are associated with the nettle batteries; but the number of the batteries in the coenosarc and at the base of the polyps appears to be greater than in Xenia or Alcyonium, and the fewness of the nematocysts on the tentacles and pinnules seems unusual. Evidently the surface of the coenosarc between the polyps is an important region for the work that the large nematocysts do. The polyp often contracts to the level of the coenosarc with the mouth still open and the tentacles still spread, and I have seen food particles passed along from the coenosarc to the mouth by the tentacles. The nematocysts of the smaller sort are more evenly distributed on the outside of the colony, but they are very few. I failed to find gland cells on the outer surface, except perhaps in the coenosarc. Von Koch ('87) does not include them in his list of ectoderm cells for Gorgonacea, but they are present in representatives of the two other alcyonarian groups. It seems hardly probable that the slime which is given off by Pseudoplexaura when it is handled has come from the mucus cells of the endoderm. The fibers of certain of the ectoderm cells of the coenosarc (Plate 3, Fig. 24) are, as has already (p. 750) been suggested, possibly supporting fibers, such as K. C. Schneider (:02, p. 622, Fig. 510) has described for Anthozoa and other invertebrates, and figured for a sea anemone.

The mesogloea of the colony is very thin except in the coenosarc region; but here is thicker than that of the forms heretofore described, except the Gorgonacea.

The endoderm is similar to that of Alcyonium, and shows no significant features, except the absence of muscle fibers in the longitudinal canals. Menneking (:05), from the study of Stachodes and other forms, reached the conclusion that the longitudinal canals have originated as inter-mesenterial chambers of a terminal polyp. The absence of muscles in the walls of the longitudinal canals of Pseudoplexaura, in contrast with their presence in the mesenteries, together with the fact that the canals are sometimes traced to solenia without polyps, suggests that in this form the longitudinal canals have not originated in this way. Kinoshita (:10) did not succeed in finding muscle fibers in the endoderm of the longitudinal canals

of the developing colonies of Anthoplexaura, but in the growing part he found solenia, which were sometimes continuations of the longitudinal canals. The structure of adult Pseudoplexaura supports the conclusion of Kinoshita, that the longitudinal canals have not always developed from inter-mesenterial chambers.

Structures Concerned in Nutrition.

Though I often experimented with small portions of a colony in the laboratory, I saw very little feeding. Plankton was given, but I saw none of it stunned, and only the smaller less active organisms, such as sea-urchin eggs, were swallowed. Sea-urchin eggs and small pieces of the flesh of fish were placed near the polyps and were often taken into the stomodaeum. Sometimes a polyp kept large pieces of sea-urchin ovary against its mouth for a long time. Usually the whole colony was quite fully expanded, except when it had been vigorously treated. On the reefs colonies with all the polyps contracted were very seldom seen. In the laboratory I could not find any difference in the condition of a colony at night and in the daytime in this respect. Individual expanded polyps may have the peristome closed, or polyps that are contracted so that the tentacles are spread out on the coenosarc may show it open; but there seems to be no special time for feeding. I think the food is undoubtedly from the plankton, and particularly the smaller and more sluggish forms.

The nettle cells of the smaller kind (Plate **2**, Fig. 31, *cl. nm'cys.'*; Plate **4**, Fig. 47) are very abundant in the ectoderm of the stomodaeum, while less numerous on the tentacles. Those of the larger kind (Plate **2**, Fig. 26, *cl. nm'cys.*; Plate **4**, Figs. 43–46) are most abundant in the coenosarc between the polyps and are seldom found in the tentacles. When sea-urchin eggs are scattered with a pipette over the tip of a branch whose polyps are expanded, they fall slowly, and do not seem to be stopped by tentacle or polyp, but collect in the grooves of the coenosarc. Associated with the falling of sluggish material on the coenosarc, adjacent individual polyps often contract down to the level of the coenosarc with the tentacles still partly spread and the mouth widely open. In such cases the eggs are often drawn into the current of the siphonoglyph. The supporting cells of the stomodaeum have at times small irregular granules at the distal end. These may be zymogen granules or, more probably,

products of metabolism destined for other than enzyme use. Food material may be taken into these cells, and even algae have been found in them in a partially digested condition. Some of the food, then, is probably digested here, both in an intra-cellular and extra-cellular fashion. After the remaining food passes the stomodaeum it is in contact with the six ventral mesenterial filaments. These (Plate 4, Fig. 64) are very short thickenings of the margins of the six mesenteries, and occupy a position immediately below the stomodaeum. They are less than two millimeters long and in preserved material may be less than one. They begin at the deep end of the stomodaeum, but their gland cells may be found on the mesenteries a little above this. The cross section shows that this thickened margin is nearly cylindrical. The cells are mostly gland cells that are not different from the granular cells of the stomodaeum. A few supporting cells occur among the others and these may contain food matter. There are no nettle cells.

Until 1899, the stomodaeum was considered as merely a passage for the food, the mesenterial filaments being regarded as the only digestive organs. Wilson ('84) described the filaments of eleven genera from the three groups of Alcyonaria and concluded that the six lateral and ventral filaments are derived from endoderm and that the two dorsal ones are from ectoderm. The former contain gland cells and sometimes nettle cells, and are digestive in function; while the latter have two kinds of cells, are ciliated and are used for the production of currents. In 1899 Ashworth found mucous gland cells in the stomodaeum of Xenia, and correlated their presence with the absence of the ventral filaments. Miss Pratt (:05), by a very thorough and complete study of the feeding, in which she employed colored food, found that food was ingested, not only by the cells of the stomodaeum and filaments, but also by the mesogloeal cells. But no ingulfing of food was observed in the cells containing the granules. Gland cells were abundantly present in the stomodaeum of many members of the Alcyonaria, but the granular cells were met with in starved individuals only. Pseudoplexaura agrees with the forms studied by Pratt in the presence of gland cells in the stomodaeum and the abundance of the granular cells in the tips of individuals starved in filtered sea water. In Miss Pratt's experiments particles of fish artificially colored were also engulfed by stomodaeum cells, by the network of interstitial cells in the polyp wall, and by the mesogloeal cells near the outer surface of the coenosarc. Both the stomodaeum and the ventral filaments, then, are digestive structures; while the granular gland cells, which

are quite abundantly scattered in the endoderm of the coelentera, including the canals and the mesenteries, may considerably aid in extra-cellular digestion.

Dorsal Mesenterial Filaments.

These filaments differ in origin, structure, and use from the ventral and lateral filaments. As a whole, the filament is a long, deeply grooved ribbon or cord, attached to the margin of the corresponding mesentery, and reaches from the stomodaeum to the depths of the polyp cavity; if there is a large basal canal connecting polyps with one another, it may even be continued into such canals. In cross section (Plate **4**, Figs. 62, 63) the filament is much thicker than the mesentery and is deeply notched at its free margin. Consequently, in cross sections the mesogloea has the form of the letter Y. The epithelial cells occupying the space between the arms of the Y are of two kinds. The outer ones (*cl. fil.*), those nearer the ends of the arms of the Y, are the more numerous and are similar to the supporting cells of the stomodaeum. They are columnar, of small diameter and so closely packed that their nuclei are arranged in several rows. Each cell has a very strong cilium, and these cilia are so long that those of one side of the groove touch or cross those of the opposite side. The remaining cells, those occupying the base of the filament groove (*cl. fil.c.*), are few but larger, having broad bases and tapering slender necks. Their cell boundaries usually cannot be demonstrated. Near the base of each cell is a large, lightly staining nucleus. They possess no cilia. The cytoplasm is sometimes evenly granular, but often shows large vacuoles that stain with muci-carmine. The mucus, which they evidently have secreted, may sometimes be found between the cilia of the other cells.

Wilson ('**84**) has described in detail these dorsal filaments for other alcyonarians. But neither in his eleven genera, nor in the figures of Alcyonium by Hickson ('**95**), nor of Xenia by Ashworth ('**99**), are the cells represented to be as large and prominent as they are in Pseudoplexaura. I did not observe the effect of the presence of mucus in this groove, save that sometimes very minute particles, presumably of food, may be found in it; the mucus is probably for the purpose of catching material entering the polyp from another polyp or from the long canals. Portions of colonies kept for some days in the dark or in weak light lost their Zooxanthellae. The polyps of these portions

of colonies are then translucent and the direction of the currents produced by the cilia can be detected. The current formed by the cilia of the filaments flows from the base of the polyp to the stomodaeum, while that of the siphonoglyph is in the opposite direction.

Growth.

Growth being both terminal and radial, the polyps may increase in either direction. The tips formed in summer are of two types. One type shows no polyps on the terminal two or three millimeters of the branch, which is crowded with purple spicules. In only a very few instances were polyps formed at the tip of the stem in this type in any other position than the radial one. They were usually large and of the same size. This is not an area of reproduction of polyps at this time. The other type of stem shows a tip denuded of polyps for a relatively long region, one half to one or more centimeters. The coenosarc wall of this tip is smooth and many of the polyps nearest to the denuded region are small. Under the surface of this tip is found an extensive network of canals. Very small polyps are also often found in the coenosarc at other regions than that of the tip. Young polyps, then, may be found in the growing stem in all parts of the colony.

Muscles and Nerves.

The arrangement of muscles into systems is not markedly different from that described for Alcyonium by Kassianow (:**08**). The systems are: (1) The tentacle and disk system. This is ectodermal. The muscle fibers (Plate **2**, Fig. 5, *my'nm.*) run longitudinally on the pinnules (Fig. 6) and on the tentacles (Figs. 5, 7) and are continued on the disk toward the mouth, but the lateral strands of each of the eight bands bend outward to be inserted in the mesogloea of the mesentery. The median strand on the oral side of the tentacle is continued to the mouth, but these muscles are fewer than in Alcyonium. The aboral surface of the tentacle, as is shown by a transverse section (Fig. 7; compare Fig. 21), bears no muscles, and muscles are lacking on a very small portion of the aboral surface of the pinnules (Fig. 6). (2) The polyp-wall system embraces muscles that are endodermal and are arranged circularly (Fig. 20). They are strongest where the polyp wall and tentacles meet, and they may pass a slight

distance on to the base of the tentacles. In the small canals (as in Fig. 56, *my'nm.*) they are generally circular. (3) The stomodaeum system. Endodermal muscles are feebly developed in the stomodaeum, where they run circularly (Plate **3**, Fig. 30). At the oral end, and to a less extent at the coelenteric end, they are larger and more numerous, but hardly enough so to be termed sphincters. (4) The mesentery system. These are, of course, endodermal. The longitudinal muscles, on the ventral side of the mesogloea (Fig. 33. Compare Plate **1**, Figs. 2–4), are independent of the epithelium. The folding of the mesogloea, which in cross sections appears branched, is such as to accommodate a large number of fibers without a corresponding increase in the width of the mesenteries. Transverse muscles are found on both sides of the mesentery (Fig. 33); they are comparatively few and are arranged in a single sheet, i. e., without foldings.

Physiologically the muscles may be divided into, first, the longitudinal muscles of the ectoderm of the tentacle and disk and the strong longitudinal endodermal muscles of the mesenteries; secondly, the circular endodermal muscles of the polyp wall and canals together with the transverse muscles of the mesenteries.

The nerves can hardly be said to be arranged in a system, as they surely are in colonies of more active alcyonarians. Sense cells are found, particularly in connection with the nettle batteries, and ganglion cells are scattered in the deeper layer of the ectoderm of both column and stomodaeum. But there is no conspicuous nerve layer, such as that found by Kassianow (:**08**) in Alcyonium.

The weakness of the nerve layer accords with the slowness of the polyps in contracting. These do not respond to touch as quickly as many other related forms living near them, such, for example, as Euniceopsis, Plexaura and Gorgonia. The tentacles show no response to a single light touch, but a sharp touch, or one repeated, gives a reaction, which is always toward the mouth, as is to be expected from the fact that the muscles are limited to the oral side. The response of one tentacle, however, is accompanied by a response of the other seven. The disk and column respond to touch, and the column responds more quickly and vigorously near its base than elsewhere. But the coenosarc between the polyps is the most sensitive part of the colony to touch. When this region is stimulated, the adjacent polyps respond by a slow contraction toward the level of the coenosarc; the response, however, is more certain than when the column is touched. There seems to be no nerve system connecting polyps

with one another, since touching one does not result in a response from another. One can draw a pencil across a branch and get a contraction of the polyps only in that line, if he does not shake the branch. When a branch is shaken, all polyps begin to contract, although very slowly. I saw no reactions that would indicate taste as contrasted with touch. Food particles on the coenosarc cause the contraction of the polyps near it, the mouth and tentacles remaining expanded; but clean filter paper does the same. Neither in the field nor in the laboratory did I find muscular response to light. The polyps were expanded night and day alike. In the laboratory, away from the sunlight they lost the Zooxanthellae and became white after a week's time.

Skeleton and Axis Epithelium.

The structure of the axis skeleton has already been described under General Structure (p. 742). I find the axis epithelium (Plate **4**, Figs. 54, 58, (*e'th. ax.*) always present and made up of two types of cells, the secreting cells and the holding cells, or desmocytes. The secreting cells are long and cylindrical or prismatic. Of the two ends, the one directed toward the skeletal axis may be designated as axis-end and the other as mesogloea-end; the former is flat, the latter tapers and is more or less rounded (Fig. 54). The large feebly staining nucleus is nearly in the middle, but typically somewhat closer to the axis-end of the cell. The cytoplasm is vacuolated at the mesogloea-end, but near the axis it is finely granular. This type of axis cell is always found at the tip of a branch, where the horny rim of the axis chambers is very thin; and I interpret this as a place of most active secretion. In any region of the colony, except at the very tip, some of the epithelial cells — sometimes only one, sometimes a comparatively large area of them — are modified into desmocytes (Plate **4**, Fig. 41, *dsm'cy.*). These cells are broader than the secreting cells at the axis-end, and relatively shorter. At the axis-end they show a prominent border of striations perpendicular to the surface. These striations are due to slender rod-like differentiations of the cell, which seem to be the means by which the cells hold firmly to the axis, even when, in sections cut either free hand or after imbedding, the other cells are detached. Where the outline of the cell is complete (*dsm'cy.*), a nucleus like that of the secreting cells is present. Often, however, the cell has united with the mesogloea so that the boundary between the two is gone, and then the nucleus may have disappeared (*dsm'cy'.*). The axis-face

of the cell (Figs. 41, 60) is usually flat, but may be concave (Fig. 58) or convex (Fig. 42). The desmocytes arise, or at least attain their differentiation, in the secreting epithelial layer. Cells in contact with the axis (Figs. 41, 58, *dsm'cy.*), that apparently are at first not different from the secreting cells, broaden their axis-end, pushing other cells away from the axis. To such a cell a mesogloeal process, probably secreted largely by adjacent epithelial cells, becomes applied, so that the cell then appears to be simply a prolongation of the mesogloea. The nucleus of the cell persists for a long time, but often it degenerates. Meantime the differentiation of the broad end of the cell shows it to be a desmocyte. Secretion on the part of the surrounding cells may continue around these desmocytes. Figure 42 shows that in this case much of the secreted layer of the axis was formed after the differentiation of the desmocyte and while it was still functioning as a hold fast. Figure 52 (*dsm'cy'.*), compared with Figure 42, shows evidence that the axial portion of the desmocyte may lose its connection with the mesogloea owing to the constriction of its neck by the formation of the horny secretion. It is in this way that some of the smaller chambers of the axis-cortex are formed. When this has taken place, other desmocytes appear in the same region peripheral to it.

In places where a great many desmocytes have been formed (Plate 4, Figs. 58, 60), the secreting cells are pushed back from the secreting surface in disarray. The displacement is perhaps a necessary result of the broadening of the ends of the desmocytes. At a later time, perhaps in response to the same stimulus that causes the beginning of a new skeletal chamber in places where desmocytes do not occur, such displaced secreting cells rearrange themselves preparatory to the secretion of a new lamella, leaving a lenticular space between themselves and the previously secreted portions of the axis. Later still, some sort of stimulus may then cause other desmocytes to appear among these secreting cells, probably as the result of the differentiation of a part of their own number. I consider these holding cells to be homologous to those seen by Fowler in a madreporarian coral and to those whose origin was described by Bourne ('99) for the madreporarians and for Heliopora, an alcyonarian with a calcareous skeleton; but I find no reference to similar cells for any other alcyonarian, except that possibly A. Schneider (:05, p. 128) found them; but if so, he evidently thought them artifacts. I have found them in all the colonies of Pseudoplexaura studied, and I have also seen them in the species of Euniceopsis and Gorgonia which are associated with

them on the Bermuda reefs. In Pseudoplexaura the stimulus for the change from the secreting cell to the desmocyte must be irregular; it is not associated with any particular position of the polyps or with any structure that would give a regular pull or strain, since the cells occur sometimes in broad patches and sometimes singly; the latter are completely united with the mesogloea and are therefore fully formed. They remind strongly of the desmocytes described for the madreporarians by Bourne ('**99**), but there is no trace of the membrane which Bourne found between cell and axis. In their origin they also differ from those described by Bourne for Heliopora, where the stimulus for the striations occurred before the cells were in contact with the axis, to which they became adjacent secondarily; for in Pseudoplexaura the first trace of the striations is in cells already touching the axis. It should be noticed that in the present paper the desmocytes have been shown clinging to a horny skeleton, whereas previous researches have shown them only in connection with calcareous skeletons. Probably further study will show desmocytes present in a large number of alcyonarian forms.

The origin of the horny skeleton of the Gorgonacea has been the subject of much controversy, with which the names of von Koch, Studer, and A. Schneider have been prominently associated. A. Schneider (:**05**) has reviewed the literature carefully, and has shown that Ehrenberg, Dana, Milne-Edwards et Haime, and von Koch have maintained an ectodermal origin; while Lacaze-Duthiers, Kölliker, Studer, and Heider have not found the ectoderm involved. The arguments against the ectodermal origin, as summed up by Schneider and strengthened by his researches, have to do with (1) the presence of calcareous spicules within the horny skeleton, (2) the character of the union between the axis and its branches, (3) the existence of extra-axial horny masses in the cortex independent of epithelium, (4) the increase in size of the adult axis, (5) the embryonic origin of the skeleton.

Kölliker ('**65**, pp. 163–167) argued in part as follows: since the axis skeleton in certain forms (Mopsea) is composed exclusively of fused calcareous spicules, and since these spicules are not produced by epithelium, the skeleton is not an epithelial product. Studer ('**87**) and A. Schneider (:**05**) found numerous calcareous spicules in the axis, and thought the axis made up principally of them. I have found no evidence of such spicules in the axis of Pseudoplexaura, though I have found one or two instances of cellular matter that I conceive to have been included in the axis owing to the rearrangement of the secreting

cells of the axis epithelium over a mass of desmocytes, and I can account for the possible enclosure of spicules in an axis in the same abnormal manner.

A. Schneider found that in Eunicella the axis of the branch (Nebenaxis) is at first separated from that of the stem, with which, however, it is later united. It is difficult to see how such an axis can be explained as the result of the secreting activity of an ectodermal epithelium, except in cases in which the branch is secondarily united (by anastomosis) to a stem, as in fan corals; but Eunicella does not usually have such a secondary union of branch and stem. Perhaps, however, the conditions in Eunicella are not essentially different from those which are met with in Pseudoplexaura, where I find that a sharp demarcation line between the axis of the branch and that of the stem also occurs (Plate **4**, Fig. 61); here it is due to the fact that all branches of the axis are adventitious in respect to the marrow. At the region of branching, the marrow of the stem-axis is separated from that of the branch by the secreted cortex of the stem-axis. The walls of the marrow chambers in the branch were therefore formed after the axis-cortex of the main stem possessed an appreciable thickness (Fig. 61, *ctx. ax.*). But the existence of a stem-cortex between the marrow chambers of the stem and those of the branch is not inconsistent with an ectodermal origin of the epithelium secreting the axis of the branch, because axis-cortex is formed in the same manner as axis-marrow. In both cases the horny matter is laid down in the form of walls of chambers; and these differ only in the size and shape of the cavity and in the thickness of the wall. The chambers of the axis-cortex are smaller than those of the marrow, nevertheless they vary greatly among themselves in size (Fig. 57, *ctx. ax.*). It is assumable that, after some of these axis-cortex chambers of the stem had been formed (Fig. 61, *ctx. ax.*), other chambers with the characteristically thinner walls and larger cavities of the marrow, may have arisen at the place where a branch was about to be produced. The walls of these chambers would, then, be secreted by the same epithelium that recently had been building smaller chambers as an axis-cortex of the stem. The epithelial patch at the distal end of the axis of the branch would be composed of cells which had changed somewhat the character of their secretions, so that henceforth they would produce the larger thin-walled chambers characteristic of the marrow, whereas the remaining cells (at first situated in the periphery of this terminal patch) would continue to produce the smaller chambers, with thicker walls, such as they had been producing as axis-cortex of the stem; but now as the axis-cortex of the branch.

In no part of the axis of a stem or branch has the marrow grown in opposite directions, part distally, part proximally, for the walls of the chambers are always convex toward one end of the stem or branch — the distal end (Plate **4**, Figs. 57, 61). The marrow must therefore have grown from the base of the branch toward the tip, just as it does in the stem from base toward tip, and not, as maintained by some writers, in the form of a separately established axis which grows in two directions: partly toward the tip and partly toward the stem to which, in their view, it is destined to be attached secondarily.

This type of axis — with the axis-cortex interposed between the marrow chambers of stem and branch — is the natural one for all axes except such as may have been formed by the dichotomous branching of a main stem. Such branches may possibly occur, but my dissections have not shown any. Occasionally, in colonies that had attained a height of ninety or more centimeters, the beginning of a branch was found on some of the whips. These, as short as five millimeters, had a soft axis that was continuous with the main axis and was formed of the characteristic marrow (Figs. 57, 61, *med. ax.*) and a very thin cortex. The marrow chambers were separated from those of the main stem by the cortex region of the stem-axis and, as has already been stated, were convex toward the free end of the branch, as in the main branch they were convex toward its free end. Although the earliest stage in the formation of the axis of a branch has not been seen in Pseudoplexaura, I am convinced that the axis skeleton of the whole colony in this species is not produced by a coalescence of separately established axes.

Pseudoplexaura gives no evidence on the third of Schneider's points, for no horny substance has been found in the coenenchyma. But the real issue between the two theories of ectodermal or non-ectodermal origin hinges on the results of observation as to the origin of the axis and as to the method of its subsequent growth; whether it is an epithelial secretion, as argued by von Koch ('**78**, '**87**), or results from a massing of mesogloeal material which is to be resorbed and replaced either by horny substance or horn and lime. Von Koch has described ('**87**) a larval stage of Eunicella a week old and has shown sections having the ectoderm continuous with the axis epithelium. His results have recently been confirmed by Kinoshita (:**10**) in embryos of Anthoplexaura. Kinoshita not only found the ectoderm of the pedal disk continuous with the axis epithelium, but he also has described and figured (Fig. 3–5) the beginning of the axis as a secretion product of the thickened ectoderm of the pedal disk; however, this primitive

axis (a single case) did not by its upward growth push before it the floor of the digestive cavity of the primary polyp, but rather grew upward in the wall of the column at one side, so that the primary polyp had the appearance of being a lateral outgrowth from the axis. From this he concludes that the stem of the colony in Anthoplexaura apparently does not belong to the primary polyp, but to the coenosarc (at its base), just as in Pseudaxonia.

The existence of a secreting epithelium in the adult of Pseudoplexaura cannot be doubted. The axis-secreting cells are large, and this cell layer, which is evident, can be traced in free-hand sections from the tip of the axis to the spreading base near the substratum. I always find an unbroken axis epithelium around the tip. This seems to me to be irreconcilable with the method of growth outlined by Studer, and represented by the sections shown in A. Schneider's paper. For Studer's theory demands a mass of spicules at the tip, as well as in other places, perhaps,— spicules which are later to be resorbed. These spicules must of course develop in the mesogloea, and for their incorporation into the axis would require a break in the epithelium around the tip; but such a break I have not seen in Pseudoplexaura. There is often a massing of spicules at the tip *outside* of this epithelium, but there is no trace of their inclusion in the axis, nor of their conversion into it. The spicules are here pushed aside by the growth of the axis and remain as spicules in the mesogloea. A. Schneider holds that the axis epithelium as figured by von Koch, with which the epithelium of my figures is undoubtedly homologous, is the endodermal lining of the digestive cavity of the axial polyp, into which the axis has been pushed, and that the longitudinal canals are mesenterial chambers. But so far as regards Pseudoplexaura, the cells of the axis epithelium are not like endoderm cells. Moreover, the longitudinal canals vary considerably in numbers in Pseudoplexaura tips, being eight or *more*; besides, as Kinoshita found for Anthoplexaura, they have no muscles and sometimes end in solenia.

Pseudoplexaura, then, affords no evidence of spicules included in the axial skeleton; a secreting axis epithelium is present, the cells of which are unlike those of the endoderm in their arrangement and structure. Even when pushed aside by the spreading of the desmocytes, they are not easily to be mistaken for endoderm cells. Kinoshita's evidence in the embryos of Anthoplexaura is a strong support for the ectoderm theory. The results from the study of the adult of Pseudoplexaura are not in themselves complete evidence, but so far as they go speak strongly for the ectodermal origin of the horny axis, as indicated by von Koch.

Summary.

Pseudoplexaura crassa, an alcyonarian of the group Gorgonacea, shows the character of Gorgonacea so far as regards the regions recognizable in cross sections of the branches; the branches have a central horny axis, a thick coenenchyma and an outer zone of polyps. The horny axis shows a marrow composed of large chambers arranged end to end, and a peripheral layer of smaller less regularly shaped ones arranged side by side and irregularly overlapping one another. The coenenchyma has, not far from the axis, a region of large longitudinal canals. These are sometimes prolonged at their tips into solenia. The polyps are long, and have ten to twelve pairs of pinnae on each of their tentacles. They are crowded, so that when expanded they hide the coenenchyma. Groups of small, crowded, irregularly stellate, purple spicules occupy the deeper parts of the coenenchyma, and larger, spiny and spindle-shaped, usually white spicules are in its outer part. No spicules are found in the polyps.

The ectoderm has the usual cover cells, nematocysts, sense cells, and interstitial, ganglion, and muscle cells. Small nematocysts are found in the ectoderm of the polyp's column, tentacles and stomodaeum. Large ones in considerable numbers are grouped into batteries in the coenosarc. Ganglion cells are very few, and muscle cells are found on the oral side of the tentacles and disk only. In the ectoderm of the coenosarc between the polyps some of the ectoderm cells have each a prominent supporting fiber, which runs from near the nucleus perpendicularly to the mesogloea.

The mesogloea is thin, except in the coenosarc regions, where it is very thick. Cords of cells like the interstitial cells of the ectoderm can be traced from the ectoderm to the deeper layers of the mesogloea. In these cords there are partly formed and fully formed nematocysts, spicule cells, and cells having an irregular shape and either containing granules or destitute of them. These irregularly shaped cells form a transition to the jelly-secreting cells, which are small and have many long branches. Large spicules are produced by characteristic secreting cells with large granules and one to many nuclei. Spheroidal nutrition cells occur in many colonies, but these are found in both ectoderm and endoderm; they probably originate in the endoderm of the canals which form a network through the mesogloea.

The endoderm cells are of characteristic form, being united with each other at the proximal and distal ends, but, in fixed material,

separate elsewhere. In the tentacles, in the polyp wall and in many canals they contain large numbers of the alga Zooxanthella. Except in the tentacles and the longitudinal canals, they have myonemes running circularly. Unicellular mucus glands and granular cells, that are probably digestive in function, are numerous. The cells of the longitudinal canals differ from other endodermal cells in being much longer and in having no trace of myonemes.

Digestion is accomplished by cells of the stomodaeum, by the six ventral and lateral mesenterial filaments, and by scattered gland cells in the walls of the polyp cavity and the canals. The stomodaeum has, beside its supporting cells, mucus and granular gland cells. The mesenterial filaments, except the dorsal pair, are very short and their epithelium is composed of granular gland cells only, which give some evidence of intracellular digestion. I found no special feeding time and no regular alternation of contraction and expansion of polyps. Slow-moving organisms, which serve as food, are often transferred from the surface of the coenosarc between the polyps, where large nettle cells abound, to the mouth of a polyp that independently contracted to the level of the coenosarc with its mouth open. The two dorsal mesenterial filaments are very long and sinuous and their cell structure is peculiarly significant. The sides of the groove are lined by cells with strong cilia. The central cells, however, show the character of mucus cells and produce a mucous secretion.

The muscle system is similar to that of Alcyonium. The colony is characterized by the weakness of its responses and by the fewness of its nerve elements. The response to touch is not quick, and the coenosarc between the polyps is more sensitive than the polyps themselves.

The axis skeleton is surrounded by an epithelium consisting of elongated secreting cells, and in places, of desmocytes, or holding cells, these being shorter and wider, and exhibiting striations at the axial end. These cells become connected with the mesogloea secondarily. They may become isolated as the result of being completely enveloped in the secretion of horny material by the secreting cells. The desmocytes have already been described for Heliopora and for the madreporarians. The evidence in Pseudoplexaura favors an ectodermal origin of the axis skeleton.

Bibliography.

Ashworth, J. H.

'99. The Structure of Xenia Hicksoni, nov. sp., with some Observations on Heteroxenia Elizabethae, Kölliker. Quart. Jour. Micr. Sci., vol. 42, pp. 245–304, pl. 23–27.

Bourne, G. C.

'95. On the Structure and Affinities of Heliopora coerulea, Pallas. With some Observations on the Structure of Xenia and Heteroxenia. Phil. Trans. Roy. Soc. London, vol. 186, pp. 455–483, pl. 10–13.

Bourne, G. C.

'99. Studies on the Structure and Formation of the Calcareous Skeleton of the Anthozoa. Quart. Jour. Micr. Sci., vol. 41, pp. 499–547, pl. 40–43.

Bujor, P.

:01. Sur l'organisation de la vérétille. Arch. de Zool. Exp. et Gen., Sér. 3, Tom. 9, Notes et Revue, No. 4, pp. xlix–lx, 7 fig.

Delage, Y., et Hérouard, E.

:01. Traité de Zoologie Concrète. Tom. 2, pt. 2, Paris. x + 848 p., 72 pl.

Hargitt, C. W., and Rogers, C. G.

:01. The Alcyonaria of Porto Rico. Bull. U. S. Fish Commission for 1900, vol. 20, part 2, pp. 265–287, 4 pl.

Hickson, S. J.

'95. The Anatomy of Alcyonium digitatum. Quart. Jour. Micr. Sci., vol. 37, pp. 343–388, pl. 36–39.

Kassianow, N.

:08. Untersuchungen über das Nervensystem der Alcyonaria. Zeit. f. wiss. Zool., Bd. 90, pp. 478–545, Taf. 29–31, 2 Textfig.

Kinoshita, K.

:10. Ueber die Postembryonale Entwicklung von Anthoplexaura dimorpha Kükenthal. Jour. Coll. Sci., Imp. Univ. Tokyo, vol. 27, art. 14, 13 p., 1 Taf., 3 Textfig.

Koch, G. von.

'78. Das Skelet der Alcyonarien. Morph. Jahrb., Bd. 4, pp. 447–479, Taf. 22, 23.

Koch, G. von.
'82[a]. Anatomie der Clavularia prolifera n. sp. Morph. Jahrb., Bd. 7, pp. 467–487, Taf. 22, 23.

Koch, G. von.
'82[b]. Vorläufige Mittheilungen über die Gorgonien (Alcyonaria axifera) von Neapel und über die Entwicklung der Gorgonia verrucosa. Mitth. Zool. Sta. Neapel, Bd. 3, pp. 537–550, 15 Textfig.

Koch, G. von.
'87. Die Gorgoniden des Golfes von Neapel und der angrenzenden Meeresabschnitte. Fauna u. Flora des Golfes von Neapel, Monogr. 15, Die Gorgoniden. x + 99 pp., 10 Taf.

Koch, G. von.
'91. Die Alcyonacea des Golfes von Neapel. Mitth. Zool. Sta. Neapel, Bd. 9, pp. 652–676, Taf. 25, 28 Textfig.

Kölliker, A. von.
'65. Icones Histologicae oder Atlas der vergleichenden Gewebelehre. Abt. 2, Leipzig, W. Engelmann. 4to, pp. 85–181, Taf. 10–19.

Korotneff, A.
'87. Zur Anatomie und Histologie des Veretillum. Zool. Anz., Jahrg. 10, pp. 387–390.

Krukenberg, C. F. W.
'87. Die nervösen Leitungsbahnen in dem Polypar der Alcyoniden. Vergl.-physiol. Studien, Reihe II. Abt. 4, Theil 1, pp. 59–76, Taf. 1. Heidelberg.

Menneking, F.
:05. Ueber die Anordnung der Schuppen und das Kanalsystem bei Stachodes ambigua (Stud.), Caligorgia flabellum (Ehrbg.), Calyptrophora Agassizii (Stud.), Amphilaphis abietina (Stud.) und Thouarella variabilis (Stud.). Arch. f. Naturg., Jahrg. 71, Bd. 1, pp. 245–266, Taf. 8, 9.

Pratt, Edith M.
:05. The Digestive Organs of the Alcyonaria and their Relation to the Mesogloeal Cell Plexus. Quart. Jour. Micr. Sci., vol. 49, pp. 327–362, pl. 20–22.

Schneider, A.
:05. Das Aschenskelet der Gorgoniden. Arch. f. Naturg., Jahrg. 71, Bd. 1, pp. 105–134, Taf. 5, 6.

Schneider, K. C.
:02. Lehrbuch der vergleichenden Histologie der Tiere. Jena. G. Fischer, xiv + 988 p., 691 Fig.

Studer, T.

'87. Versuch eines Systemes der Alcyonaria. Arch. f. Naturg., Jahrg. 53, Bd. 1, pp. 1–74, Taf. 1.

Studer, T.

'06. Ueber die morphologische Bedeutung der Achse der Gorgonacea. Verh. allgem. schweiz. naturf. Ges., Versam. 88, pp. 52, 53.

Verrill, A. E.

'65. List of the Polyps and Corals sent by the Museum of Comparative Zoölogy to other Institutions in Exchange, with Annotations. Bull. Mus. Comp. Zoöl., vol. 1, no. 3, pp. 29–70.

Verrill, A. E.

:07. The Bermuda Islands, Part 5, An Account of the Coral Reefs. Trans. Conn. Acad. Sci., vol. 12, pp. 204–348, pl. 28–40. (Alcyonaria, pp. 296–317.)

Wilson, E. B.

'84. The mesenterial Filaments of the Alcyonaria. Mitth. Zool. Sta. Neapel, Bd. 5, pp. 1–27, pl. 1, 2.

Woodland, W.

:05. Studies in Spicule Formation. II.— Spicule Formation in Alcyonium digitatum; with Remarks on the Histology. Quart. Jour. Micr. Sci., vol. 49, pp. 283–304, pl. 16, 17.

Wright, E. P., and Studer, T.

'89. Report on the Alcyonaria collected by H. M. S. Challenger during the Years 1873 to 1876. Report on the Scientific Results of the Exploring Voyage of H. M. S. Challenger, Zool., vol. 31, lxxii + 314 p., 43 pl.

EXPLANATION OF PLATES.

Abbreviations.

ax.	axis.
cam. pyp.	polyp chamber.
can.	canal.
can. lg.	longitudinal or nutritive canal.
cl. cd.	cords of cells in mesogloea.
cl. fil.	ciliated cells of the mesenterial filament.
cl. fil. c.	central cells of mesenterial filament.
cl. gl.	gland cell.
cl. gl.'	incipient gland cell of stomodaeum.
cl. gn.	ganglion cell.
cl. grn.	granular digesting cell.
cl. grn.'	granular cell of mesogloea.
cl. in.	interstitial cell.
cl. ms'gl.	mesogloeal cell.
cl. muc.	mucus cell.
cl. nm'cys.	nematocyst cell, large kind.
cl. nm'cys.'	nematocyst cell, small kind.
cl. nut.	nutrition cell.
cl. sns.	sense cell.
cl. spc.	spicule-producing cell.
cl. sst.	supporting cell.
cl. teg.	cover cell.
ctx. ax.	cortex of axis skeleton.
dsm'cy.	desmocyte.
dsm'cy'.	desmocyte, showing union with mesogloea.
ec'drm.	ectoderm.
en'drm.	endoderm.
e'th. ax.	axis epithelium.
fbr. sst.	supporting fiber.
fil. d.	dorsal mesenterial filament.
fil. v.	ventral (or lateral) mesenterial filament.
med. ax.	marrow of axis skeleton.
ms'enr. d.	dorsal mesentery.
ms'enr. v.	ventral mesentery.
ms'gl.	mesogloea.
my'nm.	myoneme.
nm'cys.	large kind of nematocyst.
nm'cys'.	small kind of nematocyst.
or.	oral.
ov.	ovum.
sipy.	siphonoglyph.
spc.	spicule.
spc'.	spicule of outer coenenchyma.
stmd.	stomodaeum.
zox.	zooxanthella.

Figures.

All drawings, except Figures 1 and 61, were carefully outlined with a camera lucida, and the details filled in afterwards. The magnification (except in Figures 1 and 61) is 675 diameters, unless otherwise indicated in the description of the Figure.

PLATE 1.

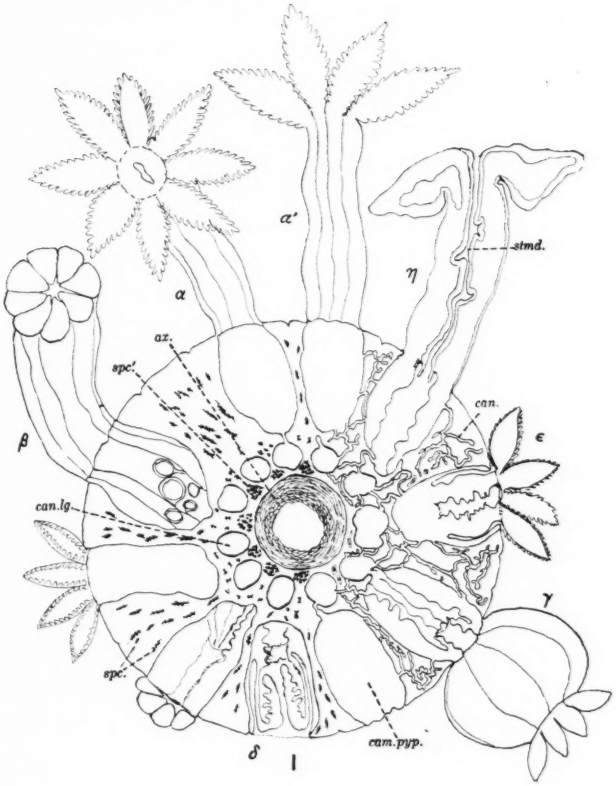
Fig. 1. Diagram of a transverse section through a branch of a colony, showing polyps in various stages of retraction.

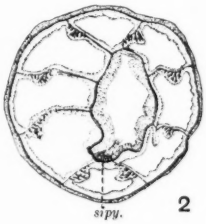
Fig. 2. Transverse section of a polyp through the stomodaeum. × 15.

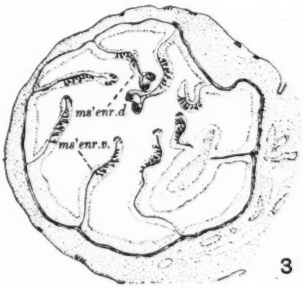
α, expanded polyp, oral aspect
α', expanded polyp, seen from the side
β, expanded polyp with inrolled tentacles
γ, polyp partially retracted
δ, polyp completely retracted
ϵ, polyp with column retracted, but with expanded tentacles and with open mouth
η, polyp in longitudinal section

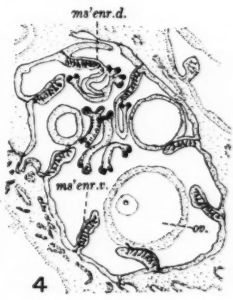
Fig. 3. Transverse section of a polyp just below the stomodaeum. × 15.

Fig. 4. Transverse section of a polyp through the lower polyp cavity. × 15.


α'
α
β
η
stmd.
az.
spc.
can.
ε
can.lg.
γ
spc.
δ
cam.pyp.
1


sipy.
2

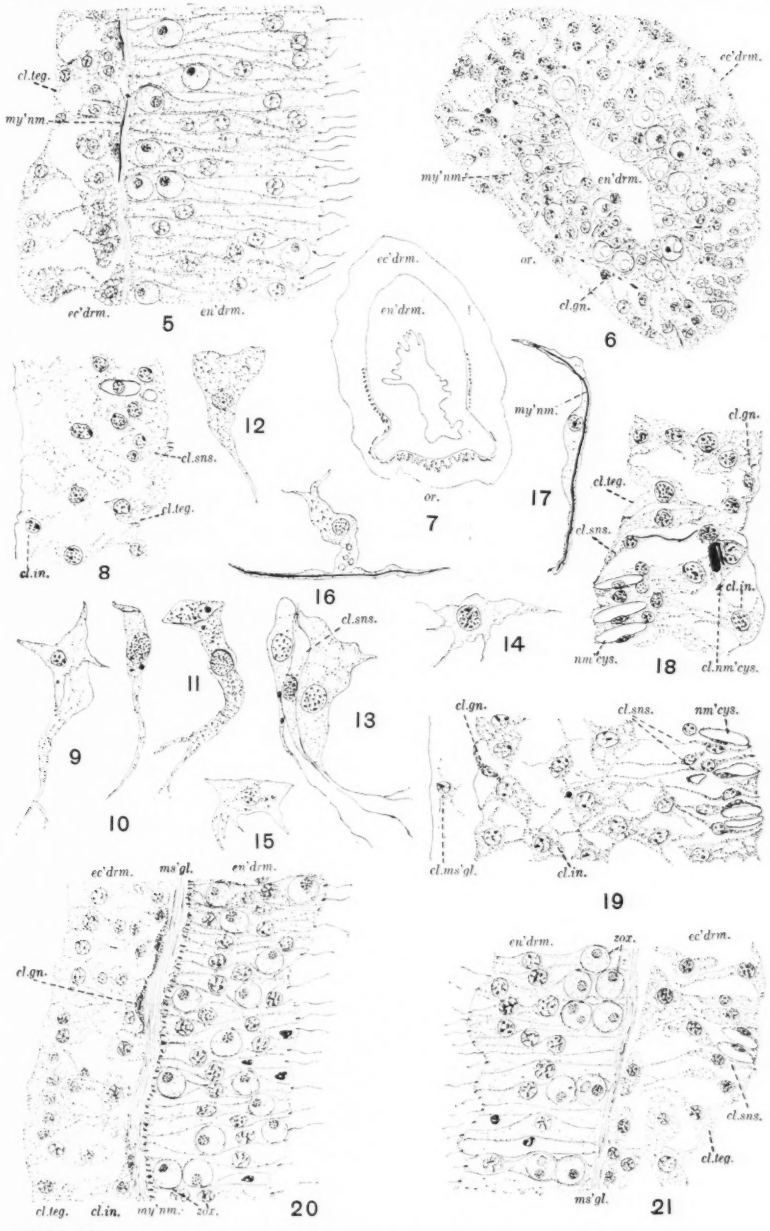

ms'enr.d.
ms'enr.v.
3


ms'enr.d.
ms'enr.v.
ov.
4

W.M.C. del.

PLATE 2.

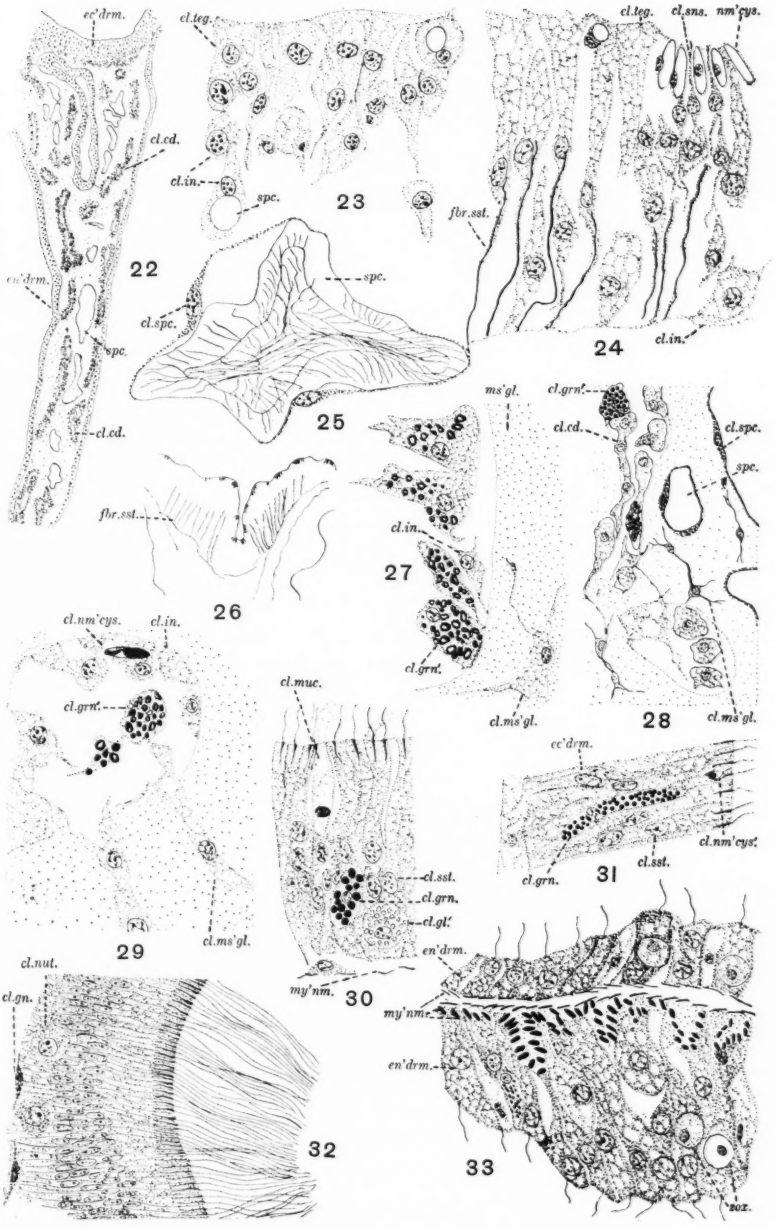
Fig. 5. Longitudinal section from the oral wall of a tentacle.
Fig. 6. Transverse section of pinnule. × 600.
Fig. 7. Transverse section of a tentacle, showing the arrangement of the muscles. × 85.
Fig. 8. Longitudinal section of ectoderm of polyp wall.
Figs. 9–12. Isolated ectoderm cells of polyp wall, drawn from maceration preparations.
Figs. 13–17. Ectoderm cells of tentacle isolated by maceration.
Fig. 13. Two cover cells and a sense cell.
Figs. 14, 15. Interstitial cells.
Figs. 16, 17. Muscle cells of the ectoderm.
Fig. 18. Longitudinal section of the ectoderm of polyp wall, in state of expansion.
Fig. 19. Section of ectoderm of the body wall of a polyp near the coenosarc.
Fig. 20. Longitudinal section of polyp wall, partly contracted. × 600.
Fig. 21. Longitudinal section of tentacle wall, aboral side. × 600.


cl.teg.
my'nm.
ec'drm.
en'drm.
5
ec'drm.
en'drm.
or.
cl.gn.
6
my'nm.
12
cl.sns.
cl.teg.
cl.in.
8
ec'drm.
en'drm.
or.
7
my'nm.
17
16
cl.gn.
cl.teg.
cl.sns.
cl.in.
nm'cys.
18
cl.nm'cys.
14
9
11
cl.sns.
13
10
15
cl.gn.
cl.sns.
nm'cys.
cl.ms'gl.
cl.in.
19
ec'drm.
ms'gl.
en'drm.
cl.gn.
cl.teg.
cl.in.
my'nm.
zox.
20
en'drm.
zox.
ec'drm.
cl.sns.
cl.teg.
ms'gl.
21

W.M.C. del.

PLATE 3.

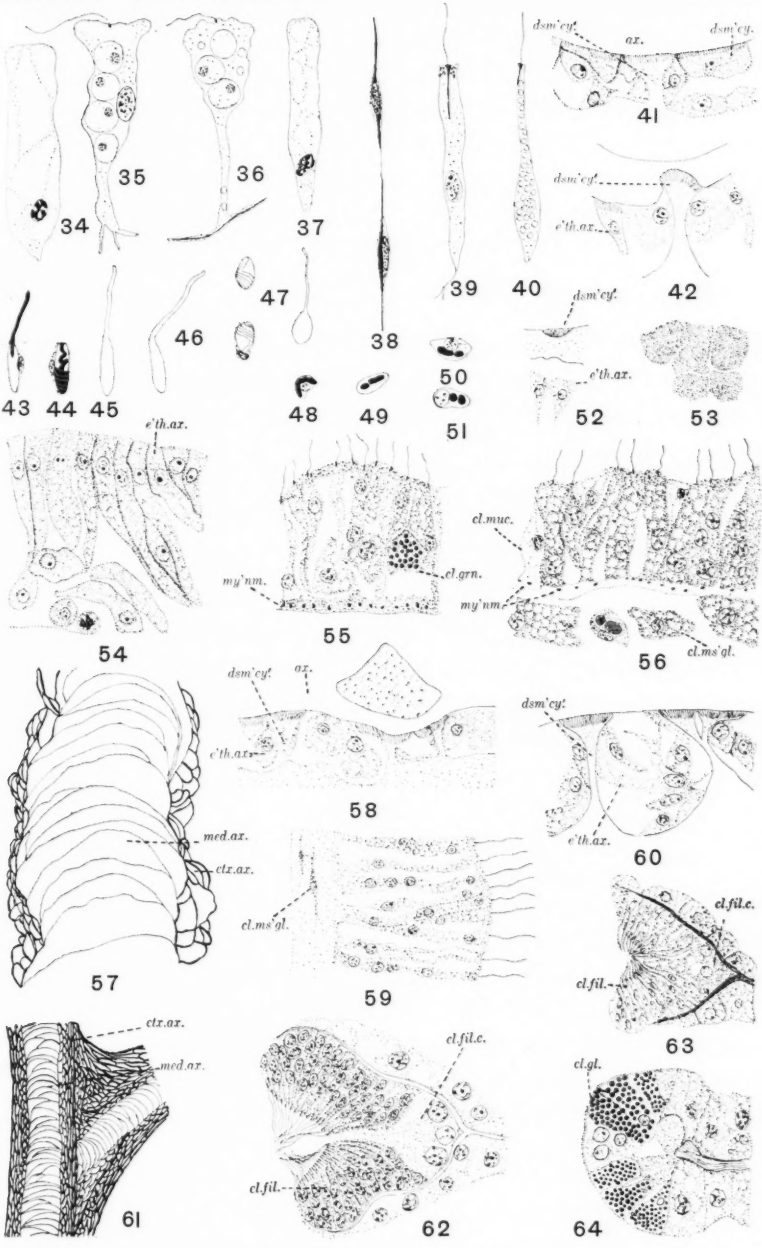
Fig. 22. Section through the coenosarc to show cords of interstitial cells. × 67.
Fig. 23. Section of epidermis of coenosarc.
Fig. 24. Ectoderm of coenosarc in the region shown in Figure 26.
Fig. 25. Section of decalcified spicule, showing spicule-producing cells.
Fig. 26. Outline of portion of coenosarc between polyps, to show the distribution of supporting fibers and of nettle batteries. × 67.
Fig. 27. Section to show mesogloea.
Fig. 28. Section showing mesogloea cells. × 400.
Fig. 29. Section of "a cord" in mesogloea of coenosarc.
Fig. 30. Longitudinal section of epithelium (ectodermal) lining the stomodaeum and of mesogloea.
Fig. 31. Longitudinal section of the wall of stomodaeum, showing both ectoderm and mesogloea.
Fig. 32. Transverse section of a part of siphonoglyph.
Fig. 33. Transverse section of a portion of a mesentery.


ec'drm.
cl.cd.
spc.
cl.cd.
22
cl.teg.
cl.in.
spc.
23
spc.
cl.spc.
25
fbr.sst.
26
cl.teg.
cl.sns.
nm'cys.
fbr.sst.
24
cl.in.
ms'gl.
cl.grn'.
cl.cd.
cl.spc.
spc.
cl.in.
27
cl.grn'.
cl.ms'gl.
28
cl.ms'gl.
cl.nm'cys.
cl.in.
cl.grn'.
29
cl.ms'gl.
cl.muc.
cl.sst.
cl.grn.
cl.gl'.
en'drm.
my'nm.
30
ec'drm.
cl.nm'cys.
cl.grn.
31
cl.sst.
cl.nut.
cl.gn.
32
my'nm.
en'drm.
33
sox.

W.M.C. del.

PLATE 4.

Figs. 34–37. Cells isolated by maceration.
Fig. 34. Gland cell of endoderm.
Figs. 35, 36. Supporting cells of endoderm.
Fig. 37. Mucus cell of stomodaeum.
Fig. 38. Muscle cells of mesentery.
Fig. 39. Supporting cell of stomodaeum.
Fig. 40. Granular gland cell of stomodaeum.
Figs. 41, 42. Axis epithelium, with desmocytes.
Fig. 43. Large kind of nematocyst cell, partly exploded.
Fig. 44. Large kind of nematocyst cell, unexploded.
Figs. 45, 46. Large kind of nematocyst cell exploded.
Fig. 47. Small kind of nematocyst cell.
Figs. 48–51. Interstitial cells containing ovoid bodies.
Fig. 52. Desmocyte enveloped in horny matter.
Fig. 53. Face view of the striated ends of six desmocytes.
Fig. 54. Secreting cells of axis epithelium.
Fig. 55. Longitudinal section of endoderm of polyp wall in the region of the column.
Fig. 56. Longitudinal section of endoderm of a polyp chamber.
Fig. 57. Longitudinal section of the axial skeleton, near the tip of a branch.
Fig. 58. Section of a portion of axis with its axis epithelium and desmocytes.
Fig. 59. Longitudinal section through the endoderm of a longitudinal canal.
Fig. 60. Epithelium of axial skeleton, with desmocytes.
Fig. 61. Diagram of a longitudinal section of the axial skeleton to show the nature of the skeleton in the region of a branch.
Fig. 62, 63. Cross sections of two dorsal mesenterial filaments.
Fig. 64. Cross section of a ventral mesenterial filament.


34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
dsm'cy.
ax.
e'th.ax.
my'nm.
cl.grn.
cl.muc.
cl.ms'gl.
med.ax.
ctx.ax.
cl.fil.c.
cl.fil.
cl.gl.

W.M.C. del.

UofM